

Mesozooplankton community structure in the Scotia Sea during the CCAMLR 2000 survey: January–February 2000

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Abstract

An analysis of mesozooplankton community structure in the Scotia Sea was carried out, based on 123 RMT1 double oblique hauls (0–200 m) taken during the CCAMLR 2000 Survey. Standardized sample data (log abundance per 1000 m³) were grouped into taxonomic categories and subjected to cluster analysis and multi-dimensional scaling. Two ordinations were performed, the first based on a reduced taxonomic dataset (31 categories out of a full 120) obtained by pooling ontogenetic stages within species and by including only those taxa that contributed at least 4% to total abundance at any one station. This disclosed two major station groups, which separated north and south, forming ‘warm’ and ‘cold’ water communities respectively, whereas four minor groups were mainly associated with stations around the Antarctic Peninsula and within the Weddell Scotia Confluence. Mean zooplankton abundance (238 000 individuals per 1000 m³) within the northerly group G1 was up to 12 times higher than in other groups. The second ordination using all taxonomic categories disclosed an additional intermediate group (G1a), which was geographically consistent with the southern part of the northern group 1 from the previous ordination. However, because of taxonomic similarities between all the major station groups it was concluded that they represented a single community, which differed only in its phenological development and the mass occurrence of patchily distributed organisms such as krill larvae. Testing the relationships of station groups with the position of water masses and frontal boundaries indicated that the Weddell Front was broadly coincident with the boundary of the northern and southern communities over much of its length. However, the presence of stations belonging to group G2, to the north of the Weddell Front, to the west of the Antarctic Peninsula, and around the South Sandwich Islands, was consistent with the distribution of ice-influenced

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surface water. Low zooplankton abundance and species developmental composition suggested that this ‘community’ was largely in an over-wintered state. Copepods and euphausiids dominated the mesozooplankton throughout the study area with small copepods (*Oithona* spp., *Ctenocalanus* spp. and *Metridia* spp.) particularly abundant.

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1. Introduction

The Atlantic sector is arguably one of the best studied regions of the Southern Ocean. It was the focus for the extensive Discovery Investigations undertaken during the 1920s–1930s, and again in the early 1950s, and for many other national and international programs including BIOMASS (Biological Investigations of Antarctic Marine Systems and Stocks), which generated the First and Second International Biological Experiments (FIBEX and SIBEX). The major focus of these programs was to extend knowledge of the living resources of the Southern Ocean, particularly for Antarctic krill (*Euphausia superba*); however, parallel research greatly increased ecological understanding of other polar zooplankton and some of the factors governing their distribution. Various approaches to the large-scale characterization of plankton distributions in the Southern Ocean and their relationship to the physical environment have been advanced in recent years. Mackintosh’s (1936) initial view of the region south of the Antarctic Polar Front (APF), based on 600 samples collected between 1927 and 1931 in the top 100 m of the water column emphasized the distribution of cold- and warm-water plankton and spatio-temporal variability in its richness. Communities were distinguished that were broadly associated with different water masses; a northern zone populated by typically warm water species, a zone of permanently scarce plankton in the region of the Antarctic Peninsula, and a zone enclosing the line separating Bellingshausen and Weddell Sea faunas. Hempel (1985) reviewed the geographical distribution of plankton in the Southern Ocean and described the occurrence of latitudinal zones that were mainly determined by seasonal variations in ice cover. There are obvious parallels between this view of ecological zonation and the patterns described by Mackintosh (1936) in that the latter connected the distribution of cold-water

species and pack-ice movement. The regional oceanography developed by Longhurst (1998) based on algal ecology emphasized the importance of frontal zones within the Southern Ocean as separating ecological provinces. The annular ring between the APF and the Antarctic Divergence is synonymous with the southern branch of the Antarctic Circumpolar Current (ACC) and was viewed as a single province with its ecology driven by the presence of krill, salps and copepods. Most recently Pakhomov and McQuaid (1996) and Pakhomov et al. (2000) have described the distribution of zooplankton communities along transects running from the region of the Sub-tropical Convergence across the Southern Ocean to the Antarctic Continent in which the major fronts variously serve to delimit and define community structure. However, some frontal features such as the Southern Antarctic Circumpolar Current Front (SACCF) and the Southern Boundary of the Antarctic Circumpolar Current (SBACC) have only recently been described (Orsi et al., 1995), and their importance in terms of zooplankton dynamics and distribution has not been assessed. The ACC in the Atlantic sector is a very dynamic region and downstream of Drake Passage meandering of frontal zones and eddy shedding can geographically alter the distribution of plankton (e.g., Atkinson et al., 1990). Additionally, large-scale movements of water masses due to atmospheric forcing have been reported which can also fundamentally alter plankton distributions (e.g. Priddle et al., 1988) and more recently there has been speculation about the affect ENSO (El Niño Southern Oscillation) events might have on large-scale distribution (Quetin et al., 1996).

Unlike the Indian Ocean sector where a number of large-scale oceanographic surveys have recently taken place (see Chiba et al., 2001; Hosie, 1994; Hosie et al., 2000), there have been few opportunities to assemble a comparably large-scale view of

the Atlantic sector. The survey sponsored by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR)—the CCAMLR 2000 Survey—covered an extensive area (approximately 15 degrees of latitude and 50 degrees of longitude) and under normal circumstances a synoptic view of the plankton over such a large area would have been difficult to achieve without temporal aliasing of the data. However, the four-ship survey enabled all the observations to be obtained in only 29 days. Analysis of the resulting 123 RMT1 samples collected over an area stretching from the South Sandwich Islands through the Scotia Sea and down the western side of the Antarctic Peninsula—an area of just over 2 million km²—has provided a synoptic basin-scale view of plankton distribution and made it possible to investigate community structure and to assess the importance of frontal regions as community boundaries.

2. Methods

Double oblique rectangular mid-water trawl (RMT8+1) samples (0–200–0 m) were taken as part of a suite of standard netting protocols carried out at each station (Watkins et al., 2004). Nets were towed for an average of 32 min (quartile ranges 27–39 min), and the resulting samples, or in some cases subsamples, were preserved in 10% v:v formalin in seawater and shipped to the UK for subsequent analysis. This paper presents results based on an analysis of samples taken with the smaller of the two nets; the RMT1 (1 m² mouth area, 330 µm mesh). Once in the UK, large species such as krill, salps, and other gelatinous forms were removed. Samples were then split using a folsom plankton splitter into a series of aliquots. Two fractions of between a $\frac{1}{2}$ to $\frac{1}{64}$ of the preserved amount were usually counted to ascertain the numbers of larger mesozooplankton (copepods, chaetognaths, euphausiid larvae etc.) and two fractions usually between $\frac{1}{256}$ and $\frac{1}{512}$ were counted for the smaller end of the spectrum (Oithiniids, *Ctenocalanus* spp., copepod nauplii, etc.). Data were standardized to abundance per 1000 m³ based on flow rates determined from flow meters

placed in the RMT8 nets. It is known that the RMT1 can fish independently of the RMT8 and presents a mouth area to the water, which is dependent on ship speed (Pommeranz et al., 1983). During this survey the average speed of the net through the water for all deployments was 2.25 kn (quartile range 2.04–2.53 kn) at which speeds the mouth area ranges from around 0.5 to 0.65 m² (mean \sim 0.6 m²). Data were standardized accordingly.

A total of 120 taxonomic categories were enumerated including species, species stages, genera, or in some cases higher taxa. Copepods were the dominant organism (67 taxonomic categories) along with euphausiids (22 taxonomic categories). Data were analyzed using the statistical package Plymouth Routines in Multivariate Ecological Research, PRIMER 5 (PRIMER-E Ltd 2000) see Clarke and Warwick (1994). Copepod species stages and larval euphausiids were initially pooled within species to give overall totals, thus reducing the dataset to 77 taxonomic categories. Standardized data were log-transformed and a similarity matrix created containing those zooplankton that contributed $\geq 4\%$ of the total abundance at any one station which further reduced the list to 31 taxa (Field et al., 1982). Data were then subjected to nearest neighbor clustering using the Bray-Curtis dissimilarity index and non-metric multidimensional scaling and station groups arbitrarily identified. These groupings were then subjected to the ANOSIM (analysis of similarity, analogous to one-way ANOVA) and SIMPER (similarity percentages) routines to determine the significance of differences between groups and to identify the species contributing to similarity within, and differences between, groups. The routine BIOENV (see Clarke and Ainsworth, 1993) was used to test the extent to which measured environmental variables (mean temperature in the top 50 m, salinity, density, latitude, and surface chlorophyll) accounted for pattern in the species data, and BVSTEP (see Clarke and Warwick, 1998) was used to test for redundancy in the taxonomic dataset by seeing if a limited subset of species could produce the same pattern.

The same procedure was then performed on the full (unpooled) dataset to investigate whether the

inclusion of ontogenetic species stages altered the basic patterns which resulted from the initial analysis.

3. Results

3.1. Community structure

Results of clustering analysis and multi-dimensional scaling on the reduced dataset are shown in Fig. 1.

Two main groups (G1 and G2) were identified as a result of clustering the data, containing 60 and 44 stations, respectively, and a further four groups (G3 to G6) with 7, 7, 3 and 2 stations, respectively.

When overlaid on the survey area the two largest station groups (G1 and G2) showed strong geographic integrity, with G1 occupying the northernmost part of the survey area and forming a boundary with G2 to the south, broadly along the line of the Weddell Front (WF) (Fig. 2). However stations belonging to G2 also were found on the western side of the Antarctic Peninsula and around the South Sandwich Islands suggesting that this was a cold-water community and was influenced by the extent of ice-influenced surface waters (see Brandon et al., 2004). The four minor groups (G3–G6) were geographically consistent with neritic waters around the South Shetland Islands and also water influenced by the Weddell Scotia Confluence. Mean zooplankton abundance within G1 was up to 12 times higher than in the additional groups (Table 1 and Fig. 3).

Differences between stations grouped in this way were tested using the statistical routine ANOSIM. Overall the station groups derived from clustering were shown to be a robust way of grouping the data. The null hypothesis that there were no differences between groups was not supported by the global R statistic ($R = 0.726$) and values of R in all pairwise comparisons between the major groups and minor groups were all >0.615 ($p = 0.001$).

Analysis of similarity (SIMPER) was carried out to establish which species were responsible for similarities within and dissimilarities between groups. Data from the first ordination are

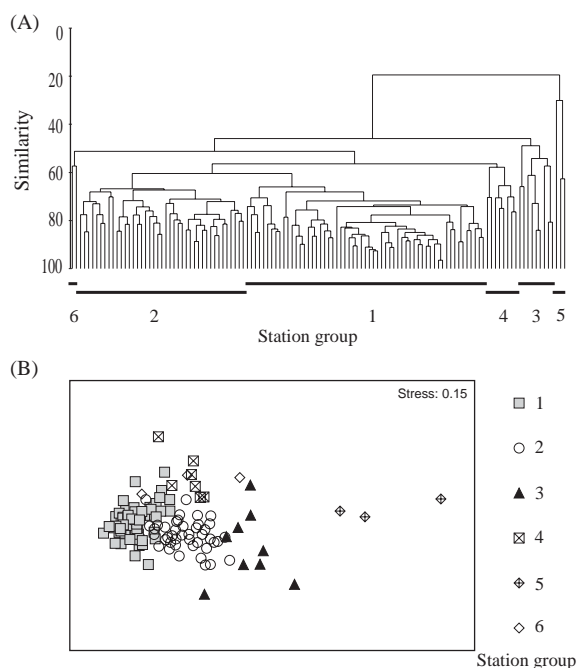


Fig. 1. Identification of station groups based on the results of (A) Bray–Curtis Clustering of the reduced species by station data matrix. Station labels have been omitted for clarity; and (B) non-metric multi-dimensional scaling ordination of the reduced species by station matrix.

summarized in Table 2 where mean abundance (individuals per 1000 m³) of the 23 taxa which contributed $\geq 4\%$ to within-group similarity or between-group dissimilarity are presented. The listed taxa accounted for $>90\%$ of within-group similarity across all groups. The two largest groups (G1 and G2) were more similar in taxonomic composition than any other of the group comparisons (average dissimilarity = 39.52) and differences were primarily accounted for by species that were more abundant in G1, reflecting the increased zooplankton abundance in this group and the more northerly distributions of many of its component taxa e.g. *Limacina helicina*, *Calanus simillimus*, *Rhincalanus gigas* and *Clausocalanus laticeps*. G3 and G5 were both characterized by relatively low abundance and although G5 contained many of the species serving to characterize G1 and G2, it was dominated by the swarm-forming zooplankton *Thysanoessa macrura*, *Euphausia superba*, and *Salpa thompsoni*

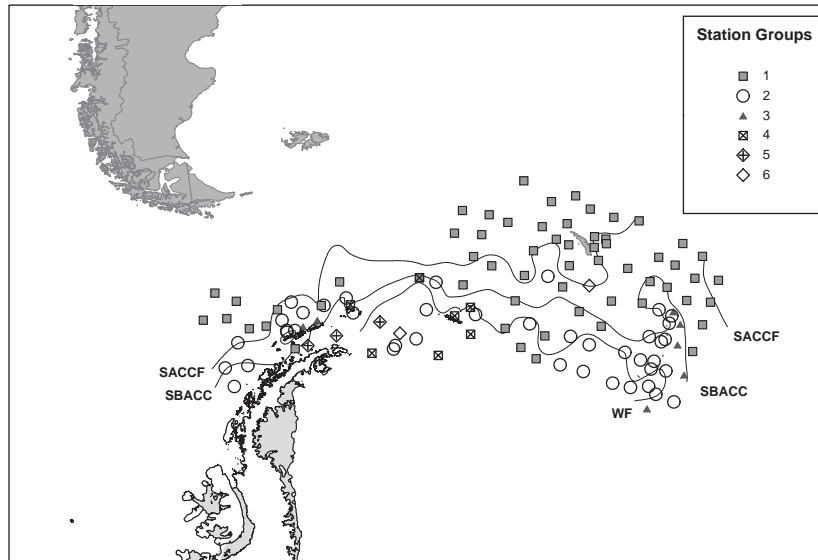


Fig. 2. Distribution of station groups derived from the reduced species by station ordination. Positions of fronts from north to south are: the Southern Antarctic Circumpolar Current Front (SACCf), the Southern Boundary of the Antarctic Circumpolar Current (SBACC), and the Weddell Front (WF).

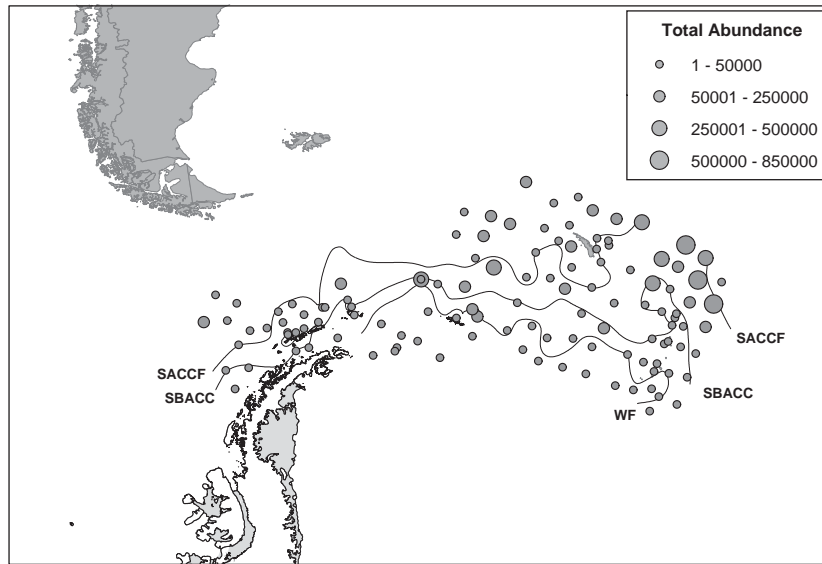
Table 1
Zooplankton abundance (individuals per 1000 m³) by station grouping for the reduced ordination

| Station group (no. sites) | Mean abundance | Median abundance | Upper quartile | Lower quartile |
|------------------------------|-------------------|---------------------|-------------------|-------------------|
| G1 (60) | 238 578 | 107 256 | 39 571 | 359 891 |
| G2 (44) | 61 698 | 16 761 | 3822 | 76 276 |
| G3 (7) | 33 653 | 7433 | 1837 | 59 610 |
| G4 (7) | 99 104 | 33 407 | 14 328 | 268 857 |
| G5 (3) | 20 442 | 9940 | 323 | 51 002 |
| G6 (2) | 28 061 | 28 061 | — | — |

blastozooids. G4 encompassed a number of stations occurring between the tip of the Antarctic Peninsula and the South Orkney Islands and was distinguished from all others by the high abundances of *Euphausia superba* larvae.

An ordination of stations based on the full selection of species stages was also performed, i.e., without pooling stages within species, or selecting those that contributed a certain percentage of the abundance. This time five groups were identified in the log-transformed data, with three containing in

excess of 30 stations and two with seven and four stations, respectively. The northern G1 was smaller than previously, and its boundary was now approximately coincident with the SACCf. G2 was also smaller and mainly restricted to the area around the South Sandwich Islands. An intermediate group (G1a) was present to the south of the SACCf, which now incorporated a number of stations from the southern part of G1 in the first ordination and others that were previously found along the southern perimeter of the survey area (Fig. 4). Stations within this group were characterized by many of the small copepod species such as *Ctenocalanus* spp., *Oithona* spp., and all stages of *Metridia* spp., which were also common in G1, as well as the younger and intermediate stages of some of the biomass dominant copepods such as *Calanus propinquus* CII and CIII and *Calanoides acutus* CIII. It was distinguished from G1 by the presence of *Euphausia superba* calyptopis stage 1 and reduced numbers of the more northerly distributed *Thysanoessa vicina*, *Scolecithricella minor*, and *Calanoides acutus* CV (Table 3). With minor changes, the remaining groups were largely as identified in the first ordination.

Fig. 3. RMT1 total abundance (individuals per 1000 m³) by station.Table 2
Reduced dataset

| Species | G1 | G2 | G3 | G4 | G5 | G6 |
|------------------------------------|---------------|--------|------|---------------|-----------|-------------|
| <i>Oithona</i> spp. | 87 316 | 7752 | 78 | 243 | <1 | 40 |
| <i>Euphausia superba</i> larvae | 8287 | 10,462 | 4550 | 42 947 | <1 | 69 |
| <i>Metridia</i> spp. | 40 384 | 4629 | 565 | 3465 | 2 | 2366 |
| <i>Calanoides acutus</i> | 16989 | 4143 | 56 | 22 518 | 7 | 5796 |
| <i>Ctenocalanus</i> spp. | 35 926 | 2327 | 38 | 2040 | 1 | 111 |
| <i>Limacina helicina</i> | 16 669 | 130 | <1 | 16 | 0 | 432 |
| <i>Thysanoessa</i> spp. Calyptopes | 2375 | 920 | 9 | 675 | 0 | 560 |
| <i>Thysanoessa vicina</i> | 6322 | 652 | 7 | 1536 | 3 | 2684 |
| <i>Calanus simillimus</i> | 11 036 | 11 | <1 | 0 | 0 | 187 |
| <i>Calanus propinquus</i> | 3025 | 1162 | 85 | 2450 | 4 | 4221 |
| Copepod nauplii | 10 546 | 36 | 0 | 0 | 0 | 0 |
| <i>Oncaea</i> spp. | 8965 | 728 | 12 | 0 | 0 | 0 |
| <i>Rhincalanus gigas</i> | 6018 | 196 | 14 | 73 | 1 | 1351 |
| <i>Pelagobia longicirrata</i> | 4030 | 231 | 4 | 774 | 0 | 0 |
| Chaetognaths | 2215 | 998 | 35 | 419 | 3 | 133 |
| <i>Rhincalanus gigas</i> nauplii | 3394 | 19 | <1 | 42 | 1 | 0 |
| <i>Scolecithricella minor</i> | 1233 | 248 | 74 | 108 | 0 | 138 |
| <i>Euchaeta antarctica</i> | 602 | 346 | 49 | 315 | 0 | 129 |
| <i>Thysanoessa macrura</i> | 452 | 197 | 348 | 95 | 73 | 7 |
| <i>Clausocalanus laticeps</i> | 934 | 7 | <1 | 13 | 0 | 67 |
| <i>Salpa thompsoni</i> | 37 | 119 | 224 | 318 | 73 | 0 |
| <i>Euphausia superba</i> | 17 | 39 | 41 | 56 | 38 | 3 |
| <i>Limacina</i> spp. | <1 | 9 | <1 | 12 | 22 | 0 |

Mean abundance (individuals per 1000 m³) by station grouping of those species that contributed $\geq 4\%$ to within-group similarity or between-group dissimilarity. Highest values emboldened. Species/taxa ranked according to mean abundance summed across all groups.

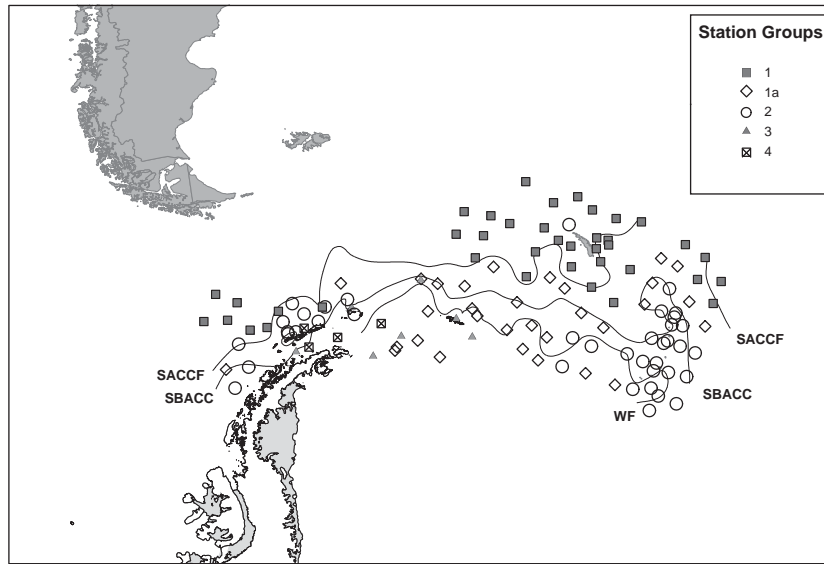


Fig. 4. Distribution of station groups derived from the full species by station ordination. Fronts as defined in Fig. 2.

Table 3
Full dataset

| Species | G1 | G1a | G2 | G3 | G4 |
|--------------------------------------|---------------|-------------|------|-------------|-----------|
| <i>Oithona</i> spp. | 47 054 | 40945 | 3974 | 73 | 2 |
| <i>Ctenocalanus</i> spp. | 22 281 | 13601 | 839 | 741 | 7 |
| <i>Metridia</i> spp. CIV-CVI | 13 372 | 11781 | 537 | 1381 | 10 |
| <i>Metridia</i> spp. CI-CHH | 8269 | 9717 | 533 | 38 | 1 |
| <i>Euphausia superba</i> Calytopis 1 | 36 | 9120 | 577 | 1671 | <1 |
| <i>Calanoides acutus</i> CV | 5368 | 2540 | 290 | 155 | 2 |
| <i>Calanoides acutus</i> CIV | 2645 | 2452 | 34 | 2867 | 1 |
| <i>Thysanoessa vicina</i> | 4549 | 2049 | 130 | 530 | 2 |
| <i>Calanoides acutus</i> CHH | 1050 | 3140 | 14 | 2976 | 0 |
| <i>Thysanoessa</i> spp. Calytopes | 1370 | 1678 | 112 | 175 | <1 |
| Chaetognaths | 1050 | 1741 | 233 | 198 | 2 |
| <i>Calanus propinquus</i> CHH | 604 | 1086 | 43 | 398 | 1 |
| <i>Scolecithricella minor</i> | 813 | 451 | 102 | 94 | 0 |
| <i>Calanus propinquus</i> CII | 149 | 840 | 39 | 79 | 0 |
| <i>Calanus propinquus</i> CIV | 369 | 418 | 15 | 102 | 1 |
| <i>Thysanoessa macrura</i> | 263 | 115 | 205 | 75 | 33 |
| <i>Salpa thompsoni</i> | 29 | 32 | 74 | 263 | 35 |
| <i>Euchaeta antarctica</i> CII | 66 | 226 | 81 | <1 | 0 |
| <i>Euphausia superba</i> | 13 | 1 | 27 | 40 | 29 |
| <i>Limacina</i> spp. | <1 | 3 | 5 | 2 | 10 |

Mean abundance (individuals per 1000 m³) by station grouping of those species that contributed $\geq 4\%$ to within-group similarity or between-group dissimilarity. Highest values emboldened. Species/taxa ranked according to mean abundance summed across all groups.

The PRIMER routine BVSTEP was used to identify the smallest subset of taxa in the reduced species by station matrix, which could explain most of the pattern in the data. This identified a subset of 19 of the original 31 species/stages in the

matrix ($\rho = 0.953$). Seventeen of these taxa (along with Ostracoda and *Euphausia frigida*) were previously identified as contributing strongly to within-group similarity and between-group dissimilarity (Table 2). With the exception of *Salpa*

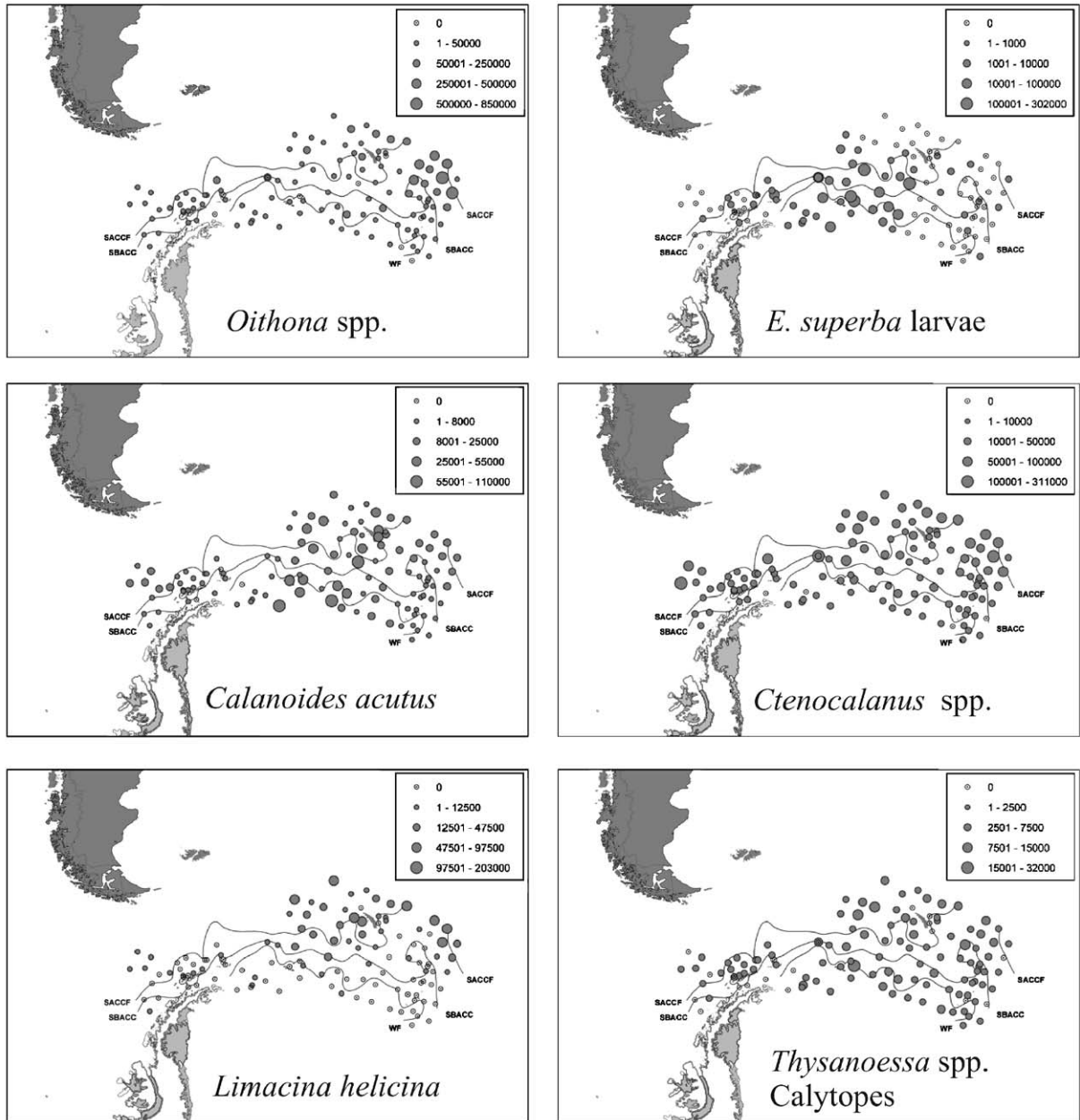


Fig. 5. Species by station abundance. The twelve species that were common to the SIMPER and BIOENV analyses (see text for further details). Fronts as defined in Fig. 2.

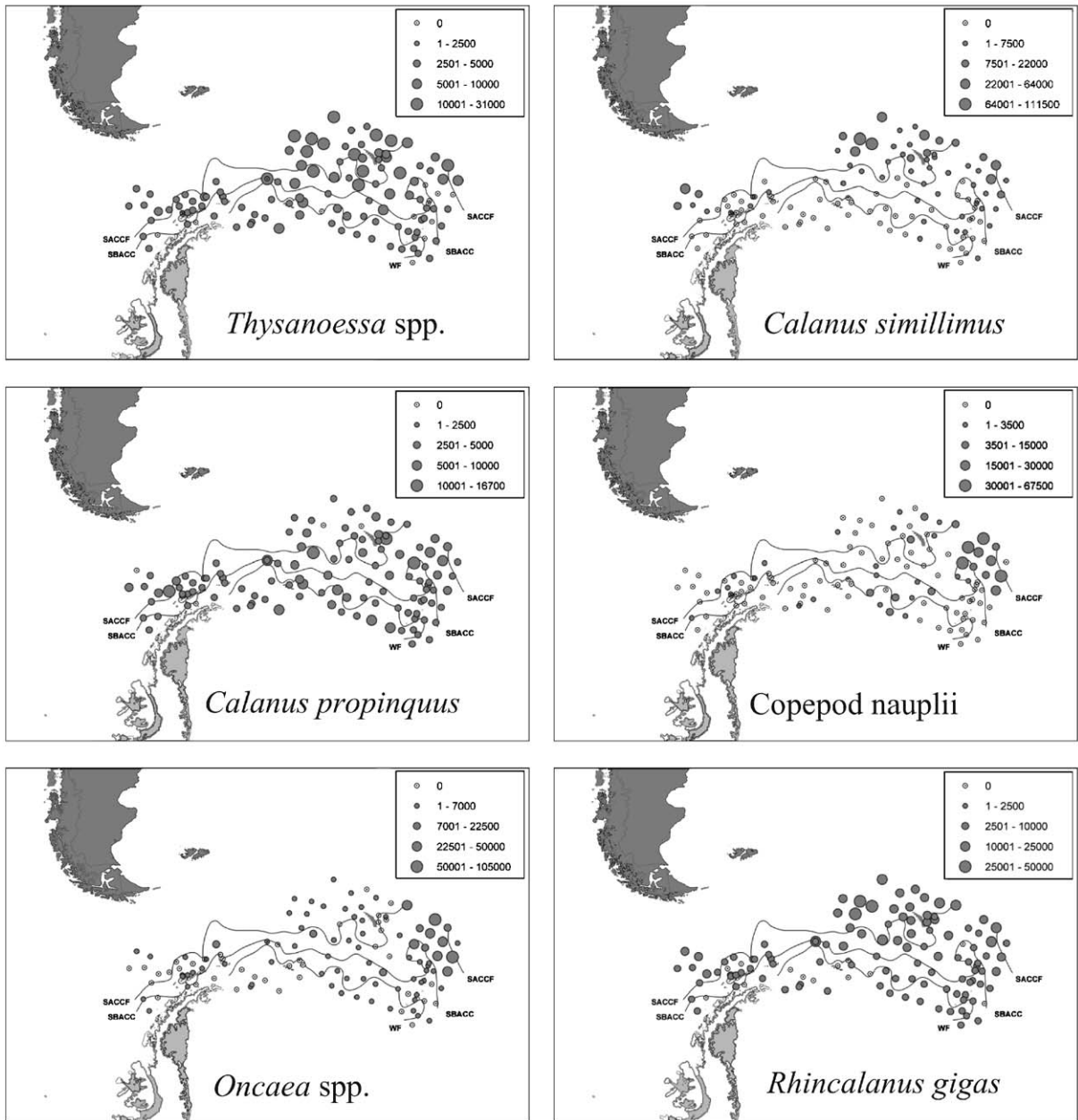


Fig. 5. (Continued)

thompsoni (distribution described by Kawaguchi et al., 2004) their distributions are presented in Fig. 5, as they describe much of the variation between station groups. Distribution patterns of these taxa fell into three basic types; those that were abundant in the north of the survey area, e.g.,

Limacina helicina, *Rhincalanus gigas*, and *Calanus simillimus*; those abundant to the south, e.g., *Euphausia superba* larvae and *Calanus propinquus*, and a number of other taxa, which despite varying enormously in abundance, were nonetheless widespread.

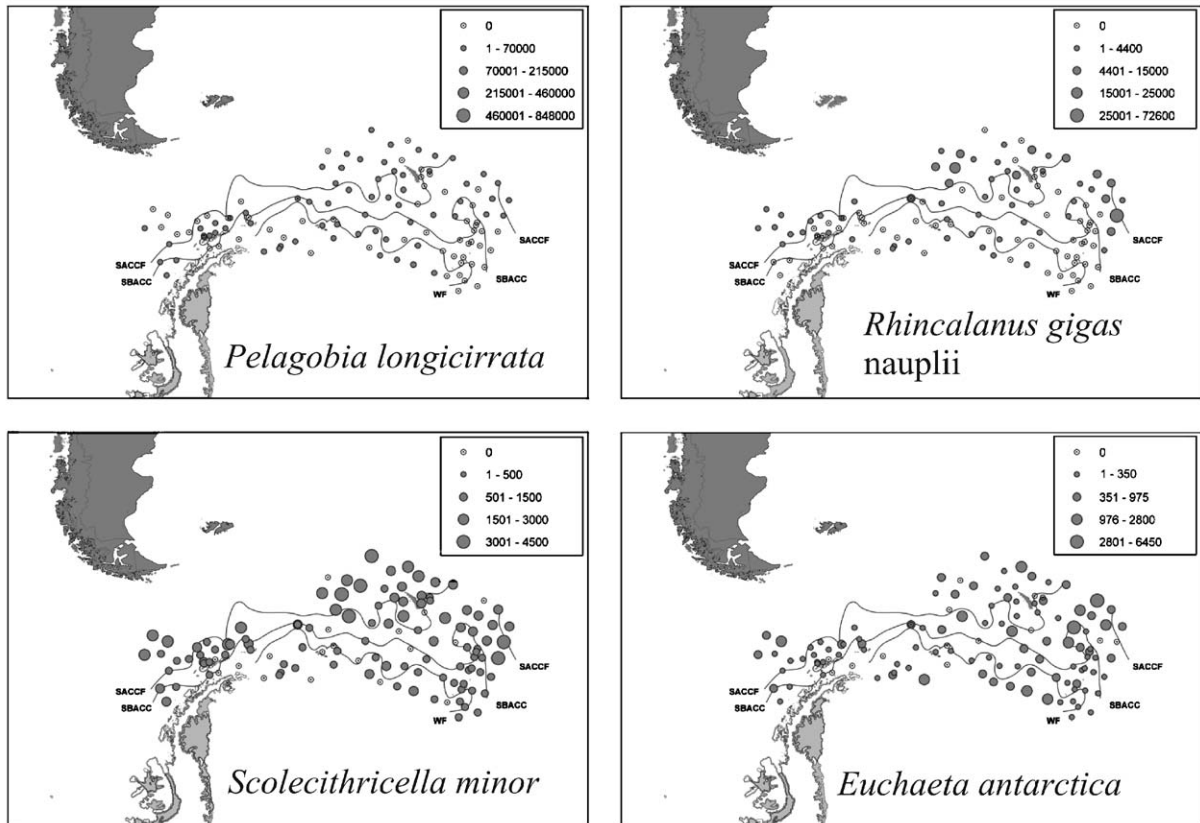


Fig. 5. (Continued)

3.2. Relationships with water mass distributions and environmental factors

To test the robustness of grouping the stations on the basis of the water mass in which they occurred, each station was characterized according to where it lay in relation to the main frontal positions (Brandon et al., 2004). Global R for both ordinations was considerably lower than for the original station groupings ($R = 0.175$) and significant differences only existed between the grouping of stations corresponding to the northern part of the ACC (mainly G1) and those to the south of the SBACC ($R = 0.323$) and the WF, which comprised mainly stations from G2 ($R = 0.303$). On this basis it can be concluded that the original grouping of stations (Fig. 2) was most robust and that the SACCF in particular had little overall effect on community structure.

Further analysis using the BIOENV procedure was undertaken to assess the correspondence and significance of environmental data to the station groupings. Of the environmental variables tested with the pooled species by station matrix, the best fit was for water density alone ($\rho = 0.139$), rather than in combination with any other variables. However the low values of the rank correlation coefficients indicated little relationship between density or any other environmental variable and the biotic data (see Clarke and Ainsworth, 1993).

4. Discussion

4.1. Species occurrence and distribution

Major differences in zooplankton abundance were apparent between station groups and also in

the proportions of the dominant taxa; copepods and euphausiids (see Tables 1 and 2). Within the two largest groups defined in the first ordination (G1 and G2), they accounted for ~90% of total abundance and between 53% and 75% for remaining groups.

4.1.1. Copepods

The dominance of small copepod species was confirmed throughout the study area, with *Oithona* spp. and *Ctenocalanus* spp. contributing greatly to the increased abundance in G1 (Table 1). Similar findings have been made by Sushin et al. (1985), Errhif et al. (1997), Atkinson and Sinclair (2000), Pakhomov et al. (2000), and Chiba et al. (2001). The highest overall abundances of many of the important species, *Oithona* spp., *Oncaea* spp., and *Metridia* spp., were located in the northern part of the region and to the east of South Georgia and the lowest overall abundances occurred in the vicinity of the Antarctic Peninsula (Fig. 3). Without exception all of the copepods (and many of the non-copepod taxa) that comprised $\geq 4\%$ of the total sample abundance (see Section 2) were more abundant in the northern G1 (Table 1). Presumably, here the combination of lower latitude, warmer water, and enhanced production (see Holm-Hansen et al., 2004) has promoted the recruitment of species which in Weddell Sea waters have yet, or are only just beginning to reproduce. Temporal delays of the order of three months or so have previously been found between commencement of recruitment of copepod species in the Scotia and Weddell Seas (Atkinson et al., 1997; Ward et al., 1997). In this survey the presence of copepodite stage V *Calanoides acutus* from the summer generation in the northern part of the survey area and of early copepodite stages or adult females from the over-wintered generation to the south also indicates a lag in the timing of recruitment of the order of two to three months. Such differences are often seen in this sector of the Southern Ocean, particularly where the meridional extent of the ACC is wide. Marin (1987) also found pronounced age differences for *Calanoides acutus* and *Calanus propinquus* during the Melville study (Brinton, 1985) with a younger population present in waters south of the WF.

4.1.2. Euphausiids

Euphausiids had their highest proportionate share of abundance in G3 to G5 (19–32%) with 7–9% in G1 and G2. Highest mean abundances of euphausiids were found in G4, largely as a result of *E. superba* larvae which occurred at all seven stations and contributed 12% to within-group similarity. *E. superba* larvae were also present in both of the main station groups, but were concentrated along both sides of the WF and occurred in somewhat lower abundance up to the approximate position of the SACCF (Fig. 5; see also Siegel et al., 2004). Previous work on euphausiid larvae from the Melville expedition (Brinton, 1985) has also highlighted the importance of this frontal region for reproduction in *E. superba* and Spirodonov (1995) has characterized the region as one in which krill reproduction starts early and has a variable but normally long duration. *Euphausia frigida* occurred throughout the region but were more abundant to the north of the position of the SACCF as were older calyptopes and furcilia stages. Calyptopis stage 1 was widespread but had a more southerly distribution. This is somewhat similar to *E. superba* larvae and suggests that larvae are moved north and east in surface waters. Makarov (1977) in a survey of the central Scotia Sea in December/January also highlighted the widespread distribution of larval forms but concluded that the most intense reproduction took place in the WF zone.

Thysanoessa spp. calyptopes were generally widespread, although once again furcilia and post larvae generally occurred in greater numbers further north. Previous work around South Georgia has established that the majority of these are likely to belong to *T. vicina*, whereas a separate category of large *Thysanoessa* spp. (>16 mm total length are probably *T. macrura*; see Mauchline, 1980) were concentrated at the eastern end of the survey area distributed in the region of the outflow of Weddell Sea water.

4.1.3. Other species

Chaetognaths were not separated into species or genera because in many cases they were too badly damaged to identify consistently. Nonetheless they were generally abundant throughout the survey

area, the exception being the region of the South Sandwich Islands in the cold outflow of Weddell Sea water. Mackintosh (1936) characterized them as being a warm water group that may sometimes occur in colder water.

Salp blastozoids (*Salpa thompsoni*) were one of the very few taxa that were more abundant in the cold-water community G2. They were largely absent north of the latitude of South Georgia and were concentrated in a zone straddling the WF and up to the approximate position of the SACCF. Salps are heterogeneously distributed within the Southern Ocean although Mackintosh (1936) indicated that along with *Euphausia superba* they had a tendency to occur in colder waters, although Siegel et al. (1992) and Park and Wormuth (1993) indicate a preference for warmer water masses (see also Kawaguchi et al., 2004).

The pteropod *Limacina helicina* was abundant in the north of the region with a southern boundary to its distribution that approximately followed the line of the SACCF. Previous work has established this feature as the southern distribution to the mass occurrence of this genus (Grachev, 1991, cited in Pakhomov et al., 2000).

4.2. Community structure

Overall the mean abundance of zooplankton within G1 was much greater than for G2 and higher than determined in many other studies within the ACC (see Pakhomov et al., 2000; Sushin et al., 1985). Regional studies by Foxton (1956) and Hopkins (1971) demonstrated a latitudinal decrease in mesozooplankton biomass and low zooplankton biomass seems typical of the Antarctic Coastal Current and Weddell Sea areas. Hopkins and Torres (1988) commented on the low zooplankton biomass in a study in the western Weddell Sea compared to the stations in the ACC although in a study by Boysen-Ennen et al. (1991) no difference in mesoplankton biomass was found between the Weddell Sea oceanic community and other data reported for the Southern Ocean. The remaining station groups were largely associated with the Weddell Scotia Confluence and Antarctic Peninsula regions. They were characterized by low

numbers of stations, lower within-group similarity, and with the exception of G4, much lower abundance. Previous work has indicated that this is a hydrodynamically complex area where many of the frontal zones lie close together and that consequently there is the potential for zooplankton from different sources to be present in the region (Jazdzewski et al., 1982; Piatkowski, 1989; Siegel and Piatkowski, 1990). Most however are in agreement with Mackintosh (1936) in that compared to other areas, the plankton in Bransfield Strait is impoverished (Jazdzewski et al., 1982; Mujica and Asencio, 1985; Mujica and Torres, 1982). Reasons for this have been variously ascribed to the influence of upwelling water masses (Mackintosh, 1936) or variations in ice cover (Foster, 1981). Schnack-Schiel and Mujica (1994) have reviewed the zooplankton found in this region and conclude that an oceanic community influenced by the ACC and a neritic community influenced by the Weddell Sea in Bransfield Strait and by Bellingshausen water off the Palmer Archipelago are present. Jazdzewski et al. (1982) also conclude that oceanic and continental zone communities are present in the region separated by the continental water boundary. They also found that the mean volume and abundance of plankton were much less in Bransfield Strait and inshore of the 500 m isobath compared to offshore, where it was three to four times greater. This is somewhat similar to the findings of Siegel and Piatkowski (1990), although as the latter make clear, separation of communities based simply on abundance or biomass, which can change over time, is inappropriate. Evidence for the existence of a neritic community in the Weddell Sea and around the Antarctic Peninsula has been provided by Boysen-Ennen and Piatkowski (1988) and Siegel and Piatkowski (1990), respectively. In addition to describing changes in abundance of species which also occur in the oceanic community they describe the presence of different dominant species such as *Euphausia crystallorophias* and *Pleuragramma antarcticum*.

Data obtained during this study although not as finely resolved as many of the surveys in this region show the presence offshore of Antarctic Zone and Weddell Sea influenced station groups,

although within the Bransfield Strait G3 and G5 predominate with stations from G3 extending along the Weddell Scotia Confluence to the South Orkney Islands.

4.3. Frontal regions as faunal boundaries

Deacon (1982) drew attention to the fact that the rise in surface temperature from the Antarctic continent northward is not uniform. A number of sharp transition zones exist in addition to the break between the continental shelf and deep water, and these frontal regions often appear as discontinuities in the distribution of phytoplankton and zooplankton (Errhif et al., 1997; Pakhomov and McQuaid, 1996; Pakhomov et al., 2000). This analysis initially suggested that two main zooplankton groups were present, broadly separated along the line of the WF. This broad boundary zone is the product of the mixing of waters of three different origins (ACC, Bellingshausen Sea, and Bransfield Strait) interacting with water from the Weddell Sea. It is a mobile feature and is characterized by meanders and eddy-like structures, particularly to the east of the South Orkney Islands, where it becomes very diffuse (Foster and Middleton, 1984). For some taxa it is reported as the southernmost limit of distribution e.g. the copepods *Calanus simillimus* (Kanaeva, 1968; Marin, 1987; Vladimirovskaya, 1978) and *Clausocalanus laticeps* (Jazdzewski et al., 1982; Marin, 1987), and is an important spawning area for at least two species of euphausiid: *E. superba* (Brinton, 1985; Marr, 1962; Siegel et al., 2004; Spirodonov, 1995) and *E. frigida* (Brinton, 1985; Makarov, 1977). Marin (1987) viewed the WF as an important boundary in terms of the abundance and age structure of zooplankton populations, but concluded that it did not separate two distinct communities as the order of abundance of species did not differ significantly. A similar conclusion was reached by Siegel et al. (1992).

Within the Scotia Sea a number of full depth frontal features have been observed (Orsi et al., 1995) all lying close together in the region immediately downstream of Drake Passage, before diverging further eastward (Brandon et al., 2004).

A number of studies have emphasized that the APF marks an important transition between subantarctic and Antarctic fauna and that the WF (continuing as the Antarctic Divergence in other sectors of the Southern Ocean) between the oceanic and continental shelf communities (Boysen-Ennen and Piatkowski, 1988; Deacon, 1982; Hosie et al., 2000; Longhurst, 1998). However while fronts may reflect distinct changes in some species distributions, for many others, they do not represent a boundary (Atkinson and Sinclair, 2000; Mackintosh, 1960). In an analysis of copepod distribution taken from the surface to 1000 m, in waters ranging from the subantarctic to the Weddell Scotia Confluence, Atkinson and Sinclair (2000) discounted Deacon's suggestion of the APF as a biogeographic boundary. They found some species to be more abundant within the front itself, rather than it representing either the northern or southern limits to distributional ranges. They concluded that there was no indication of species clustering into warm- or cold-water types and that a continuum existed between the two extremes. In the Indian Ocean sector of the Southern Ocean Errhif et al. (1997) investigated copepod composition and community structure on a transect running past Kerguelen and Heard Islands towards the Continent. They found highest densities in the region between the APF and the Antarctic Divergence with peak abundance in the region of the Antarctic Divergence. Increased abundance within fronts is commonly seen as they are often productive (see Fransz and Gonzalez, 1997; Lutjeharms et al., 1985; Pakhomov et al., 2000) or may act to physically concentrate plankton (Franks, 1992; Voronina, 1970). A transect of closely spaced stations run from Cape Town to Sanae in the Atlantic sector resolved four major station groupings separated by three major frontal systems: the Subantarctic Front, APF, and Sub-Tropical Convergence (Pakhomov et al., 2000). Within the group south of the APF a further three subgroups were apparent, the first associated with the Marginal Ice Zone and a further two in the Polar Open Ocean Zone, roughly separated by the Northern Extension of the Cold Water layer which coincides with the northernmost extent of the 0 °C isotherm and

approximates to the northernmost limit of winter sea ice. The latter feature appears synonymous with the SACCF, and according to Pakhomov et al. (2000) approximates the northern limit of Antarctic krill distribution and the southern limit of *Salpa thompsoni*, although in the Atlantic sector there is considerable overlap in the distribution of both species (see Kawaguchi et al., 2004; Mackintosh, 1936). Nonetheless their analysis, like that of Marin (1987) suggested the existence of a single oceanic community south of the APF. Data from the present survey lend only limited support to the idea of frontal regions defining the limits to oceanic zooplankton communities in this sector of the Southern Ocean. In this case, samples were all obtained poleward of the APF and although both ordinations suggested the WF as being a feature separating the two main groups, similarities in species composition between G1 and G2 lead to the conclusion that they essentially belong to the same biological community, differing only in their degree of development, probably because of differences in the timing of seasonal productivity. Although the division between the two groups broadly followed the line of the WF, particularly west of 40°W, there was a pronounced northward extension of G2 across the front to the east. This follows the path of the outflow of Weddell Sea water (Maslennikov and Solyankin, 1980), and consequently stations north of the WF around the South Sandwich Islands also belong to G2. The second ordination also shows this as being a strong structuring feature. The presence of stations belonging to this group over the shelf and shelf break area of the Antarctic Peninsula also suggests that this is more likely to be a 'cold-water community' rather than be derived exclusively from the Weddell Sea, although Weddell Sea water is known to intrude into Bransfield Strait (Stein and Heywood, 1994). The secondary frontal features such as the SACCF and the SBACC did not appear to be important in terms of defining community structure. Ordination 2 using the full species stages dataset introduced an additional group in the Scotia Sea which lay broadly between the positions of the SBACC and the SACCF. However, the composition of

this group had distinct similarities with adjacent groups and as such was only separable in terms of differing proportions of some species stages.

The distribution of the cold, ice-affected Antarctic Surface Water (Brandon et al., 2004) fairly closely follows the boundary between G1 and G2 (Fig. 2) and may be largely responsible for differences between the two. Thus the existence of a single community modified by the presence of seasonal ice cover is indicated.

5. Conclusions

This basin scale synoptic view of zooplankton community structure within the Atlantic sector of the Southern Ocean is compatible with a number of previous studies, which have been more localized in extent (e.g., Jazdzewski et al., 1982; Marin, 1987; Siegel et al., 1992). Mackintosh (1936) has published the only study on a comparable scale, based on data compiled during four summers. Despite this difference in approach, there are strong parallels between the present grouping of stations and Mackintosh's faunistic divisions; both emphasizing the strong structuring effect pack-ice distribution and temperature have on zooplankton communities. Mackintosh (1936) also emphasized that the boundaries between his divisions were not geographically fixed and that variability was a fundamental property of 'community' composition. This is apparent from the seasonal changes he noted in the proportions of 'warm-' and 'cold-water' species and the differences in the timing of ontogenetic development with latitude. The latter is also reflected in the present dataset and in that of Siegel et al. (1992) and as 'communities' develop seasonally then temporal differences between them will vary. Movement or weakening of frontal zones may also fundamentally alter 'community' distributions (Priddle et al., 1988). Sushin et al. (1985) noted the differences in the balance of species within the Scotia Sea between seasons when the balance of water masses differed and Shreeve et al. (2002) have documented similar changes around South Georgia.

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